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Diving Behavior and Identification of Sex of Breeding Atlantic Puffins (Fratercula arctica), and Nest-Site Characteristics of Alcids on Petit Manan Island, Maine

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DIVING BEHAVIOR AND IDENTIFICATION OF SEX OF BREEDING ATLANTIC PUFFINS (FRATERCULA ARCTICA), AND NEST-SITE CHARACTERISTICS OF ALCIDS ON PETIT MANAN ISLAND, MAINE

A Thesis Presented

by

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DEDICATION

To my parents, who inspired me to be passionate about whatever I chose to do in life and who supported me along the way.

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ABSTRACT

DIVING BEHAVIOR AND IDENTIFICATION OF SEX OF BREEDING ATLANTIC PUFFINS (FRATERCULA ARCTICA), AND NEST-SITE CHARACTERISTICS OF ALCIDS ON PETIT MANAN ISLAND, MAINE

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During 2008 – 2009, we quantified foraging behavior of adult Atlantic puffins (*Fratercula arctica*) by deploying time-depth recorders (TDRs) on 18 adults and collected morphological measurements from 40 adults nesting on Petit Manan Island, Maine. Dive data were successfully retrieved from 5 birds foraging for 14 days in 2008, and 8 birds foraging for 18 days in 2009. Pooling across all birds, a total of 8,097 dives were recorded, with peaks in activity during 0400-0800 and 1600-2000, and no diving between 2100 and 0400. Mean (± SD) dives/bird/day was 276.4 (± 84.7), with dives grouped into bouts lasting 17.8 (± 31.5) minutes, consisting of 8.9 (± 3.4) dives. Dive depth was less than 15 m for 86% of the dives. Mean maximum dive depth across birds was 9.7 (± 1.7) m, with the deepest dive being 40.7 m. Females made fewer deep dives (27-41 m), had more midday dives (1000 - 1559), and their dives were spread across a greater number of bouts per day than males. Given a mean foraging trip length of 60.1 (± 38.3) minutes for 26 birds observed in 2009, we estimate that adult puffins foraged, on average, within 31 km of the colony. Morphological measures were recorded by a single observer and included body mass, wing chord, bill depth, bill length, culmen, and head-bill length, and

represented 19 males and 21 females, based on blood sample analysis. Data were analyzed using classification trees, and our final tree used culmen length and bill depth to correctly classify 34 of 40 (85%) birds (kappa = 0.695, $P < 0.01$). Use of our model can greatly improve the ability of biologists to identify sex of puffins in the field at this colony site, but variability in morphological data we collected at addition colonies indicates that future work is needed to determine its applicability throughout the Gulf of Maine. During 2009, we measured burrow characteristics of alcids and empty burrows. Breeding success and burrow characteristics were measured for nests of 104 puffins, 58 black guillemots and 4 razorbills, with burrow characteristics measured for an additional 12 guillemot and 56 empty burrows. Mean diameter of burrow openings of puffins, guillemots, razorbills and empty burrows were significantly different, and artificial puffin burrows had significantly smaller openings than natural while artificial and natural guillemot burrows had similar opening diameters. Hatch, chick, and nest success of puffins was similar among burrow types, but guillemots had higher hatch and nest success in artificial burrows. The variables we used to create models for predicting hatch and nest success for puffins and guillemots had inadequate discriminatory power to predict success.

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CHAPTER 1

DIVING BEHAVIOR OF ATLANTIC PUFFINS ON PETIT MANAN ISLAND, MAINE

1.1 Introduction

Atlantic puffins (*Fratercula arctica*) (hereafter, puffins) are believed to be limited to areas of high prey availability during chick rearing due to their relatively large body mass, small wing area, and consequently, high wing loading (Ballance et al. 2001). In the Gulf of Maine, puffins are breeding on six managed colonies, Machias Seal Island, Petit Manan Island, Great Duck Island, Seal Island, Matinicus Rock, and Eastern Egg Rock. These islands are located approximately 18 km, 4 km, 10 km, 33 km, 33 km, and 8km from the mainland. Although productivity of puffin breeding colonies in the Gulf of Maine is closely monitored (Lowther et al. 2002), no information is available on puffin foraging behavior and habitat use.

Little is known about fish distributions in the region during the breeding season, but Maine Department of Marine Resources (DMR) annual inshore trawl surveys in the spring and fall give insight into inter-annual patterns of species distributions, abundance, and mass in the region. Based on anecdotal at-sea observations of puffins near Petit Manan and Great Duck Islands, foraging areas are believed to generally be within 40 km of colonies (Laura Kennedy, *pers. comm.*). A DMR spring survey conducted within approximately 40 km of Petit Manan Island documented a moderate amount of alewife (*Alosa psuedoharengus*) of sizes suitable for puffins, more than found in 2006 and 2008, but much less than found in 2007. Similarly, moderate amounts of American shad (*Alosa sapidissima*) were found in 2009, more than found in 2008 but less than 2006 and 2007; low to moderate amounts of Atlantic herring (*Clupea harengus*) were seen in 2009, similar to levels seen in 2006 and 2007, all of which were higher than those seen in

2008; and red hake (*Urophycis chuss*) were found at low to moderate levels but much higher than seen in the previous three years. Silver hake (*Merluccius bilinearis*) were found at moderate to high levels, comparable to 2007 catches, slightly higher than 2008, and much higher than in 2006, and white hake (*Urophycis tenuis*) were found moderate to high levels, much higher than those seen in the previous three years. Northern shrimp (*Pandalus borealis*) have been found at moderate to high levels since 2006. A combination of data from trawl surveys, puffin productivity, puffin foraging behavior and habitat use is necessary for managers to understand how puffin and other seabird productivity may change in the future, and where conservation efforts should be focused for long-term restoration efforts.

Similar to razorbills (*Alca torda*), common murre (*Uria aalge*), and black guillemot (*Cepphus grylle*) breeding in the Gulf of Maine, puffins are at the southern extent of their western Atlantic Ocean breeding distribution. As with many species at the edge of their distribution, puffins are likely to be highly sensitive to changes in habitat and prey availability resulting from global climate change. In the Gulf of Maine, long-term monitoring of chick diets have shown that meals consist primarily of Atlantic herring, hake (*Urophycis* spp.*, Merluccius* spp.), and sand lance (*Ammodytes hexapterus)* (Lowther et al. 2002). During 2005, the diet of puffins nesting on Machias Seal Island shifted from herring to euphausiids (shrimp), a poorer quality food (Bond et al. 2006, GOMSWG 2006), and chicks fledged at a lower body mass (Bond et al. 2006). In 2006, food quality at Machias Seal Island was poor early in the season and puffin fledging success was 0.35 fledglings per nest, the lowest since 1995. Puffin fledging mass in 2008 and 2010 were two of the three lowest years since 1995, and between 2007 and 2010, fledging wing chord was significantly lower than the previous five years. Managers have not observed a high proportion of euphausiids in nesting puffin diets at other colonies with higher productivity levels. Changes such as these could be indications that puffin breeding success is being affected

by changes in the marine environment, and distribution and abundance of prey species, which will have the greatest impact on species, like puffins and other alcids at the edge of their breeding distribution. Information on the foraging characteristics of adult puffins reported here, paired with information on prey availability, chick diet, chick growth and climatological data would greatly enhance the ability of managers to identify potential shifts in species distributions and prepare for those changes in advance.

Until the recent development of time-depth recorders (TDRs), our knowledge of puffin dive behavior has been inferred from incidental catch of seabirds in fishing gear and from the use of capillary depth gauges to measure maximum dive depths. Near seabird colonies in Newfoundland, puffins were captured in fishing gear at a maximum depth of 60 m (Piatt and Nettleship 1985). In Witless Bay, Newfoundland, researchers used capillary depth gauges to determine that the maximum dive depth was 68 m, and the average maximum depth was 46 m (Burger and Simpson 1986). Recently, TDRs have been deployed on several species of alcids in order to provide a detailed description of their diving behavior (Hedd et al. 2009, Mehlum et al. 2001, Takahashi et al. 2008, Tremblay et al. 2003). Here we describe the first measures of dive frequency, depth, and duration for puffins breeding in the Gulf of Maine.

1.2 Methods

1.2.1 Study Area

During the 2008 and 2009 nesting seasons, we captured breeding puffins at Petit Manan Island, Maine, USA (44° 22'03"N 67° 51'51"W), an island supporting approximately 100 pairs of nesting puffins (Figure 1.1). The island also supports a diverse seabird colony of over 4000 pairs of common, Arctic and roseate terns (*Stern hirundo, S. paradisaea, S. dougallii*), razorbills, black guillemots, laughing gulls (*Larus atricilla*), Leach's storm-petrels (*Oceanodroma leucorhoa*), and

common eider (*Somateria mollissima*). Puffins began nesting on Petit Manan Island in 1986, perhaps as a result of dispersal from the nearby colonies of Machias Seal Island (62 km northeast: 6,563 pairs in 2010) and Seal Island (88 km southwest; 500 pairs in 2010). Petit Manan Island is located at the southwestern tip of the cold Labrador Current, which enters the Gulf of Maine at the southern tip of Nova Scotia.

1.2.2 Deployment of Data Loggers

We captured adult puffins from burrows that were easily observed, where traps could be safely deployed, and chicks were accessible. Puffins were captured (one per burrow) using box traps, noose carpets, and by hand once their chicks were at least 7 days old. Sample sizes were 8 in 2008 (6 males, 2 females) and 10 in 2009 (3 males, 7 females). Mass of birds was measured using a 600 g Pesola spring scale, wing chord with a 200 mm stopped ruler, and head measurements with a dial calipers. Sex was identified by DNA analysis using 1-2 drops of blood (0.05 ml = 0.1 ml) collected from the tarsometatarsal or brachial vein. If not previously banded, each bird was banded with a metal field-readable band (Porzana, Ltd) on the right leg and a uniquely numbered U.S. Geological Survey Bird Banding Lab (BBL) metal band on the left leg.

We attached a cylindrical TDR (LAT 1500 model; 2.5 g, 8 mm x 32 mm; Lotek, Inc.) to a plastic cradle attached to the BBL band using adhesive tape, and oriented the TDR parallel to the leg with the pressure sensor facing the foot to limit potential effects of acceleration on the pressure sensor (Elliott et al. 2008b, 2009a, b). The combined mass of logger, cradle and adhesive tape was 3.5 g, a value which was less than 1 % of the body mass of the smallest puffin captured. When loggers were dry, they recorded pressure (accuracy of ± 1%; resolution of 0.05%) and temperature (accuracy of 0.2° C, resolution of 0.05° C) every 30 s, and when wet, they recorded pressure every 2 s, and temperature every 5 s until the memory was full (2.8 - 6.6

d). Birds were released at the water's edge and we confirmed the wet/dry sensor was working by inspecting the TDR record for a change from dry to wet at the time the bird contacted the water. In order to minimize disturbance to birds carrying TDRs, we did not attempt to observe them at the colony. When a bird was recaptured, 5 – 339 d following TDR deployment, we removed its data logger, recorded its body mass, and released it at its nest site. Within several hours of recapture, we downloaded data from the logger to a laptop computer.

1.2.3 Nest Productivity

We conducted a census of burrows in late June, noting nest contents (egg, adult, or empty). We used a video probing system (Peeper 2000 with Peep-A-Roo video extension, Sandpiper Technologies, Inc.) to view the contents of burrows that could not be seen directly. Starting in early July, we observed burrows from observation blinds to look for adults delivering prey to chicks. When accessible chicks hatched, we visited nests every 3-5 days, weather permitting, and recorded mass (g) and wing chord (cm). During the first week of August, we visited nests to record chick status to calculate breeding success parameters. We calculated hatch, chick, and nest success for each nest. Hatch success was the proportion of eggs that hatched, chick success was the proportion of chicks that fledged, and nest success was the proportion of eggs that produced chicks that fledged.

1.2.4 Data Analysis

We performed all statistical analyses in R version 2.10.1 (R Development Core Team 2009) and dive data were analyzed using diveMove software, a customized R package (Luque 2007). We observed monotonically decreasing surface values, or drift from a surface value of zero, in nearly all records. After we identified dives, we corrected for drift using a zero-offset

correction (zoc) which allowed us to manually adjust multiple, discrete sets of data in a record, removing drift from surface readings and adjusting each dive accordingly (Beck et al. 2003, Elliott and Gaston 2009). Because puffins lift their feet into their feathers while resting at sea, saltwater switches in TDRs do not accurately measure sea surface time for puffins and thus we were unable to differentiate between time spent resting at sea, flying, and resting in the colony. We defined a dive as any descent greater than three meters (Elliott et al. 2008a,b, Elliott et al. 2009a, b, Elliott and Gaston 2009, Falk et al. 2000). The descent phase of a dive continued until less than 10 % of the critical quantile of descent rates was reached, and the ascent phase started above 10 % of the critical quantile of ascent rates (Elliot et al. 2008a, Elliott et al. 2009a). We referred to the time between descent and ascent phases as the bottom time. We only used complete days of data to identify number of dives per day, bouts of dives per day, number of dives per bout, proportion of time spent diving, dive depth frequencies, and temporal variation in dive frequency. We calculated descriptive statistics, including the mean and range of descent time, bottom time, ascent time, dive duration, dive depth, bout ending criterion, and post-dive duration, for each individual and then pooled them when appropriate.

Like many diving seabirds, puffins display a temporal clumping of dives into bouts (Wanless et al. 1988). We identified bout ending criterion (BEC), the time elapsed between the end of a bout and the start of a subsequent bout, for each bird using an empirical maximum likelihood model of a mixture of two random Poisson processes, representing short gaps between dives and longer gaps between bouts of dives (Langton et al. 1995, Luque 2007, Luque and Guinet 2007, Sibley et al. 1990). Using BEC to define bouts, we calculated mean number of dives per bout and mean number of bouts per day. We tested for differences in dive parameters between sexes and years to determine if pooling was appropriate. We used two-sample t-tests and Welch's t-tests to test for significant differences between sexes or between years in number

of dives per day, dive duration, mean dive depth, maximum dive depth, BEC, number of dives per bout, number of bouts per day, and proportion of time spent diving. We used all possible subsets multiple linear regression analysis to predict dive depth based on time of dive initiation, descent time, bottom time, ascent time, and post-dive surface time and using band number as a fixed factor and compared these simple terms with quadratic terms of the same variables. We removed dive duration from the analysis because it was highly correlated with descent and ascent times and log transformed all remaining variables. Our final model selection was based on minimizing the Akaike Information Criterion (AIC). Simple linear regression was used to predict duration of dives based on their time of initiation. We split the daily diving period into three, six-hour intervals, AM (0400 - 0959), MID (1000 - 1559), and PM (1600 - 2159), and then used a log-linear model to examine whether males and females spent differing amounts of time foraging in these intervals. We tested for independence between sex and 3 categories of dive depth [shallow (3 – 14.99 m); mid (15 – 26.99); deep (27 - 41 m)], using a log-linear model. V-shaped dives were classified as having a bottom time of 0 s (Hedd et al. 2009) and extended to 2 s to examine dives nearly V-shaped. Broadness index, an indicator of dive shape, was defined as the ratio of bottom time to dive time (Halsey et al. 2007).

Sea-surface temperatures (SST) of puffin foraging areas were calculated using a custom script we developed using Python version 2.5 (van Rossum and Drake 2001). We calculated SST based on temperatures experienced by puffins for 120 s prior to the start of a foraging bout. We calculated mean foraging temperatures for individuals and used Welch's two-sample t-tests to test for significant differences between sexes and years to determine if pooling was appropriate.

We recorded departure and return times of puffins feeding chicks during 5 - 26 July 2009 in order to estimate the potential foraging range of puffins nesting on Petit Manan Island.

Birds that we monitored were not carrying TDRs, but were assumed to forage in areas similar to those of TDR birds. We assumed that puffins flew at a constant speed of 63 km/h (Pennycuick 1987, Wanless et al. 1990), that wind speed and direction were unimportant (we did not know the direction birds flew to forage), and then calculated a maximum foraging distance for each trip. We assumed birds flew to a foraging area, spent time diving for food, and then returned to the colony. We estimated mean, maximum, and minimum times spent diving for birds carrying TDRs during 2008-2009 and used these values in our calculations of possible distances to foraging areas. Unless otherwise noted, all results are reported as mean ± SD.

1.3 Results

1.3.1 Effects of TDRs

TDRs had no significant effect on body mass of adults or on fledging success of their chicks. Starting body mass was similar among males and females (females: 413 ± 32 g, n = 9; males: 438 ± 15 g, n = 6; t = 0.0053, df = 11.946, P = 0.068) (Table 1). Neither males nor females had statistically significant mass changes while carrying TDRs (t = -0.205, df = 5, P = 0.846; and t = 2.046, df = 8, P = 0.075), and the pooled sample of males and females also showed no effect of TDRs on body mass (t = 1.035, df = 11, P = 0.323). For TDR and non-TDR nests combined, hatching success and nest success did not differ between years (X^2 = 0.623, df = 1, P = 0.43; X^2 = 0.7765, df = 1, P = 0.782), but overall chick success was significantly higher in 2009 (X^2 = 8.59, df = 1, P = 0.003) (Table 2). Chick success did not differ between TDR and non-TDR chicks in 2008 or in 2009 (P = 0.706; and P = 0.160), but for non-TDR nests, chick success was higher in 2009 than in 2008 (X^2 = 7.0139, df = 1, P = 0.008).

1.3.2 Diving behavior

We recovered 13 of 18 TDRs deployed in 2008 (n = 5, 3 males, 2 females) and 2009 (n=8, 2 males, 6 females), and all loggers contained useable data. Retrieved TDRs were carried by birds for 5 to 339 d and recorded data for an average of 3.7 d per bird, totaling 48.2 bird days of data for the study. TDRs were programmed to stop recording data once the memory was full to ensure dive data were from the chick rearing period. Overall, 13,011 dives were recorded, and 8,097 of those dives were contained within 32 complete days of data.

For dives made during the 32 complete days, 60.3 % of all dives occurred during two peaks in foraging, 0400-0800 and 1600-2000, and no dives were made between 2100 and 0400 (Figure 2). Pooling across years, females made more midday dives, and less morning and evening dives, than males ($X^2 = 49.5$, df = 2, $P < 0.001$) (Figure 1.2).

Mean number of dives per day was similar between sexes and years (t = -1.8842, df = 10.064, P = 0.089; and t = -1.5026, df = 10.741, P = 0.162) and there was no significant difference in dive duration between sexes or years (t = -0.3327, df = 10.962, P = 0.746; and t = 0.3872, df = 6.826, P = 0.710). Puffins made 256.8 (± 99.6) dives per day (n = 13, range: 126.7 – 449.0) (Table 1.3), and dives lasted 48.7 (± 3.5) s, with 90% lasting < 74 s. The top model predicting dive depth with the lowest AIC was based on band number and squared descent time (AIC = -7477). There was a statistically significant difference in BEC between 2008 and 2009 (2008 BEC = 46.98, 2009 BEC = 67.94; t = -3.5478, df = 10.73, P = 0.005) but no difference in BEC between sexes (t = 0.049, df = 6.79, P = 0.962). BEC lasted, on average, 60.0 (± 15.0) s. The number of dives per bout was similar between sexes and years (t = 1.0815, df = 5.249, P = 0.3266; and t = 0.4059, df = 4.665, P = 0.7028), and bouts consisted of an average of 14.94 (± 5.3) dives. Within bouts of diving, the range of maximum depths varied an average of 8.7 m across individuals (range: 0.1 –

27.5 m), with 52% of bouts having a range of less than 8 m, and fewer than 10 % of bouts having a range of > 17 m.

Two dives (0.025%) were classified as V-shaped dives, with remaining dives having variations of flattened bottom periods. If we extended the definition of V-shaped dives to include dives with bottom times < 2s, 10.32% (n = 836) of dives would have been classified as v-shaped. Dives with a broadness index of < 0.05 had a shape visually similar to V-shaped dives but could have contained a substantial period of bottom time if descent and ascent times were long relative to bottom time. For this reason, we did not extend the V-shape classification to specific broadness index values.

There was no significant difference in proportion of time spent diving between sexes or years ($t = -1.7724$, $df = 9.484$, $P = 0.108$; and $t = -1.0445$, $df = 9.842$, $P = 0.321$) or in the number of bouts of diving per day between sexes or years ($t = -1.7908$, $df = 10.651$, $P = 0.1017$; and $t = -0.8522$, $df = 6.929$, $P = 0.423$). Birds spent 13.5 (± 5.6) % (3.24 ± 1.34 hours per day) of their time actively diving, ranging from 5.4 to 23.7% (1.35 – 5.69 h) and diving was grouped into an average of 29.6 (± 15.2) bouts per day. When proportion of diving time is adjusted for daylight and twilight length, birds spent 20 (± 8.3) % of their time actively diving.

Puffins dove to a mean depth of 9.7 (± 1.7) m, with mean maximum depth of 27.8 (± 6.84) (range: 18.8 – 40.7 m). Fifty-four percent of dives had a maximum depth less than 9 m, 84% less than 15 m, and 96% less than 21 m (Figure 1.3). Females made more shallow dives (3 - 15 m), and fewer deep dives (15 – 27 m or 27 – 41 m), than males ($X^2 = 100.99$, $df = 2$, $P < 0.001$) (Figure 1.3). No differences in mean or maximum dive depth were noted between years or between males and females ($P > 0.05$). Dive depth was linearly related to dive duration ($R^2 = 0.478$, $df = 1$, $P < 0.001$), but not to time of day ($P = 0.852$) or rest time after the dive ($P = 0.948$).

1.3.3 Foraging Habitat

There was no significant difference in SST of foraging habitat between sexes or years ($t = 0.1946$, $df = 10.975$, $P = 0.8492$; and $t = 1.4703$, $df = 7.051$, $P = 0.1846$). Average SST of foraging habitat was 10.98 ± 0.92 °C (range: 9.6 – 12.9 °C). For 26 trips of non-TDR birds, the mean trip time was 60.11 min, with a maximum of 199 min, and a minimum of 11 min (Figure 1.4). We estimate that puffins foraged within 31.6 (± 20.1) km, with the shortest trip being within 5.8 km of Petit Manan Island (Figure 1.5). Our estimate of the mean maximum distance traveled predicts that puffins were likely feeding from the Cranberry Isles south of Mount Desert Island to the eastern side of Head Harbor Island (Figure 1.5). When we adjusted non-TDR trip times based on bout length of TDR birds and subtracted the time of a single bout from the total trip time, our estimate of mean foraging distance is 30.7 (± 20.1) km, while an estimate based on five bouts is 29.5 (± 20.1) km and 10 bouts is 27.4 (± 20.1) km (Figure 1.6).

1.4 Discussion

We investigated dive characteristics of Atlantic puffins breeding at a colony in Maine, where managers have no information on alcid diving or characteristics of foraging habitat. Studying dive characteristics of puffins in the Gulf of Maine provides an important baseline for documenting how the species may adapt to a changing environment at the edge of their range. For example, if prey becomes limited in the upper 15 m of the water column, where 84% of the dives recorded in our study were located, puffins will have to increase their foraging effort to dive deeper or fly further from the colony for prey. Understanding current behavior and how that behavior may vary as a result of changing environmental conditions could be the key to establishing new puffin breeding colonies in the Gulf of Maine.

Dive characteristics and foraging behavior have been studied for a variety of large marine animals, including whales and sea lions, as well as penguins and small alcids, which has provided the opportunity to infer behavior based on dive shape, which can lead to inferences about prey type. Dives are primarily composed of researcher defined phases of descent, bottom time, ascent, and ending with a post-dive rest time before the next dive begins. Within dives, characteristics such as time spent during each phase, maximum depth, post-dive time, broadness index, rates of ascent and descent, and symmetry of the dive can be important to inferring prey types and the ability of a species to acquire prey and react to prey behavior. Dive shape, which can be identified subjectively through visual inspection or objectively using a multivariate statistical approach, can be useful for correlating bird and prey behaviors. Dives can be isolated or grouped into bouts consisting of multiple dives. Dive characteristics, timing, and grouping of dives can be used to identify differences in foraging between sexes, years, locations, and/or species.

Dive depth determines the ability of a predator to exploit prey in the water column (Brown and Nettleship 1984, Burger and Simpson 1986). The maximum depth an organism is capable of diving to depends on the size of the organism, and their ability to store oxygen (Croll et al. 1992). The actual depth of a dive depends on the physiological constraints on the organism, location of prey, which can vary due to bathymetry, sea-surface temperature, and salinity, predator avoidance and feeding behavior. Depth of dives can provide an important link to what puffins are eating and feeding their chicks and how that may vary daily or annually. Puffins have been reported to reach a maximum depth of 68 m, with a range of 22 – 68m (Burger and Simpson 1986) and birds in Newfoundland have only been caught in fishing nets set < 60 m from the surface (Piatt and Nettleship 1985). We found puffins rarely dove deeper than 20 m and reached a maximum of 40.7 m, similar to puffins in Norway, which dove to a mean

maximum depth of 26.4 (± 15.3) m (Barrett and Furness 1990). The average dive duration of Petit Manan birds was much longer than reported by using sonar in Norway (Axelson et al. 2001) and by radio-telemetry in Scotland (Wanless et al. 1988). Average maximum depth of 44 m in Newfoundland (Burger and Simpson 1986) is deeper than we observed but birds in Newfoundland primarily feed on capelin and sand lance, while we observed birds on Petit Manan Island feeding their chicks primarily juvenile Atlantic herring and silver hake during 2008-2009.

In our study, we were able to classify 10.32% of dives as having a nearly V-shape. This indicates this proportion of dives were likely either searching dives, where puffins dove to look for- but not pursue prey, or dives for prey with a limited capability of avoiding puffins, such as euphausiids or squid. The remaining 90% of dives had at least 4 s of bottom time, which could be considered further search time, but could also be an indication of active pursuit of prey. Objective classification of seabird dives requires significant amounts of detailed information about species behavior and each phase of the dive to partition dives into meaningful shape categories (Halsey et al. 2007). As research of puffin dive characteristics continues, we will be able to classify dives beyond what we report here.

Based on our calculated foraging distances and SST, puffins were likely feeding in waters less than 100 m in depth and between 9.6 and 12.9 °C. Caution should be taken, however, when comparing diving and habitat characteristics of species across their geographic distribution without detailed information on surrounding habitat type, prey availability, or prey captured during dives. Vertical prey distribution, bathymetry and water temperature vary widely and maximum depths and SST of foraging sites may reflect the species and location of prey more than physiological diving capabilities of birds.

We did not find any significant impact of carrying a TDR on adult body mass or on chick success, and therefore believe that the TDRs did not have a large impact on the foraging behavior of puffins. We used TDRs that were < 1 % of the body mass of the smallest individual in our study (379 g), therefore minimizing the potential deleterious effect of the units. We also limited our handling time to less than 15 minutes at deployment. All birds were present at the colony during the breeding season after TDR deployment but we were unable to confirm their breeding status.

This study represents the only extensive study of diving behavior in Atlantic puffins. Maximum depths and dive duration alcids are capable of are positively correlated with their body mass (Ballance et al. 2001, Piatt and Nettleship 1985, Wanless et al. 1988, Watanuki and Burger 1999). Atlantic puffins in our study dove to depths we expected based on their body mass and dive depths reported for other alcids (Figure 1.7) and had dive durations roughly related to body mass (Wanless et al. 1988, Watanuki and Burger 1999). In Scotland mean dive duration of puffins, razorbills, and common murres was 28 ± 15 s, 35 ± 16s, and 67 ± 38 s. Puffins dove marginally more per day than rhinoceros auklets breeding in Japan but spent a similar proportion of the day diving (Kato et al. 2003, Kuroki et al. 2003). Watanuki and Burger (1999) reported the "normal" dive duration in alcids could be predicted using the equation $1.094M^{0.391}$, where M = body mass, in kilograms, which predicts a puffin weighing 420 g has a "normal" dive duration of 46.8 s, similar to the 48.7 s mean dive duration we report (Figure 1.8). Understanding that birds may be capable of diving deeper or for longer durations than reported, puffins at Petit Manan appear to be capable of diving to depths for lengths of time related to their body size.

We observed a bimodal distribution of dive frequencies that is consistent with a strategy of foraging for fish that make vertical migrations toward the sea surface at dawn and dusk. Based on anecdotal observations of chick-feeding, adult puffins fed chicks primarily in the morning and evening, when prey such as herring are likely closer to the surface than during the middle of the day, which could account for the shallower maximum depths. Juvenile Atlantic herring (< 25 cm length and < 3 years old) perform daily vertical migrations toward the surface during low light intensity at dawn and dusk to feed on zooplankton (Blaxter 1985, Stickney 1972). The bimodal foraging pattern was present in both sexes but was less pronounced in females, which made more midday dives than predicted, while males made more morning and evening dives than predicted. Ignoring midday foraging, males and females made a similar number of dives, grouped in a similar number of bouts, per day ($t = -1.942$, $df = 10.074$, $P = 0.0806$; and $t = -1.8047$, $df = 10.663$, $P = 0.0994$). This is in contrast to thick-billed murres and razorbills in Labrador, where females of both species foraged more often during twilight hours. Female puffins on Gull Island, Newfoundland spent more time away from the colony during chick rearing and provisioned chicks at higher rates than males (Creelman and Storey 1991). Although female puffins at Petit Manan are foraging more during the middle of the day, they aren't diving any more than males in the same 24-hour time period, and males are behaving similarly to female thick-billed murres and razorbills in Labrador, foraging more early and late in the day.

We anticipated more evidence of an influence of sex on chick provisioning based on the finding that female puffins at Gull Island, Newfoundland, provisioned chicks at higher rates than males, but we did not find any evidence of this. This suggests that if differences in provisioning rates do occur, they are minimal. In addition, differences in self-feeding behaviors could mask possible differences in chick-feeding at the colony. Males may be foraging for themselves and

their chicks at the same times of day, while females may forage exclusively for chicks during the morning and evening and self-feed during the middle of the day, when some prey are less abundant at the surface.

Although puffins exhibited a general bimodal temporal frequency of dives, there was considerable variation among individuals. In general, males made the majority of their dives in the morning and late afternoon/evening hours, yet one male made 32% of his dives between 1000 and 1600. On average, females made approximately 32% of their dives during midday (range: 17.42 – 46.13%), and while most females made dives in the evening, one female made no dives after 1700. In contrast to thick-billed murres breeding at Coats Island, Nunavut, which dove between 2000 and 0400 (Croll et al. 1992), no puffins at Petit Manan made dives between 2100 and 0400. At the southern extent of their breeding distribution, puffins experience decreased amount of daylight compared to their northern counterparts, and may therefore be constrained to a shorter foraging period. At Petit Manan, time from sunrise to sunset is approximately 15 hours during the chick-rearing period, with an additional 1.2 hours of twilight, when the sun is less than six degrees below the horizon. Day length at colonies in Newfoundland is similar, but further north, at Coburg Island, Nunavut, twilight extends day length to 24 hours (National Oceanic and Atmospheric Administration). For birds nesting in southern latitudes, changes in spatial or temporal food availability may have greater reproductive impacts since they have less time to feed, and therefore may be more likely to experience reproductive failure in years when food resources shift.

Within bouts of diving, the average range of dive depths was 8.5 (± 1.5) m (range: 6.07 – 12.17). In general, maximum dive depth would slowly increase then decrease within a bout of dives, suggesting birds were searching for prey early in the bout, or possibly pushed prey deeper

as they repeatedly pursued the same schools of fish. An alternative explanation of dive depth decreasing during the second half of a bout is the bird is experiencing fatigue and is unable to make a dive as deep as the previous dive. Birds surfaced, in general, for less than four seconds between dives, which is likely not enough time for muscles to fully recover before making another dive, particularly because it is thought that alcids are capable of anaerobic respiration, which generates lactate that takes time to be oxidized from muscles in addition to oxygenation from aerobic diving activities (Mori 2002).This explanation, however, does not explain the slow increase in dive depth during the first half of the bout.

Our estimates of foraging distance should be considered overestimates because we are assuming the birds flew in a straight line to and from the colony and our adjusted foraging distance takes into account only 1-10 bouts of foraging. Like thick-billed murres, puffins may fly to their final foraging destination indirectly, visiting multiple foraging locations on the way from and returning to the colony (Benvenuti et al. 1998). Thick-billed murres were also shown to have foraging paths which were rectangular in shape rather than straight lines to and from the colony (Benvenuti et al. 1998). This behavior would decrease our foraging distance estimate substantially. Without a better understanding of how puffins behave on individual trips we were unable to perform further adjustments on our estimate; however, if puffins behave similarly to murres, and we apply the ratio of 2.62 (total trip distance/straight line distance) recorded by Benvenuti et al. to our puffin trip data, our estimate of foraging distance would be within 12.0 (± 7.7) km of Petit Manan Island, or from the eastern side of Schoodic Island to the western side of Flint Island. A seabird observer based on a whale-watching boat that regularly travels in the waters surrounding Petit Manan Island regularly observed puffins within our estimated foraging ranges based on 1-10 bouts of diving (Laura Kennedy, *pers. comm.*). Our initial estimate gives managers at the Petit Manan colony a conservative estimate for where they can expect chick-

rearing puffins to forage and where future foraging research efforts should be focused. Based on anecdotal observations at the colony, adults often returned to the colony with food twice during peak feeding times. This information combined with an average number of approximately 30 bouts per day suggests puffins were making 7-8 bouts of dives per trip. This estimate would place puffin foraging locations within our 1-10 bout estimates of distance. The location of foraging habitat may change daily, weekly, or seasonally depending on how prey behaves with respect to temperature and salinity gradients and depending on fluctuations in the community structures of prey populations.

Since the National Oceanic and Atmospheric Administration National Marine Fisheries Service (NOAA NMFS) observer program began reporting incidental take of seabirds in 2006, there have been no documented cases of direct mortality of adult puffins in the Gulf of Maine by commercial fishing practices. Puffins in the Gulf of Maine feed their chicks Atlantic herring, hake, sand lance, and euphausiids and our data show peak foraging times close to sunrise and sunset. Although there has been no evidence of direct mortality of adult puffins by commercial fishing vessels, puffins and fishermen compete for similar resources and commercial fishing can directly impact puffin prey and have indirect impacts on younger age classes of fish, which are more commonly fed to chicks. For example, Maine landings of Atlantic herring totaled 56,236,442 pounds worth $8,529,543 in 2010 and a five-year average of 88,290,428 pounds worth $10,705,459. In addition, Atlantic herring are a migratory fish, so fishing practices anywhere in the Gulf of Maine can have indirect impacts on puffins at colonies in Maine. In addition to environmental variables, the sustainability of the harvest will likely determine future prey availability for puffins during chick-rearing.

Globally rising ocean temperatures have been documented by researchers (IPCC 2007), and salinity in the Gulf of Maine is currently in a decreasing trend (GOMCME 2010) which could have an effect on puffin breeding success if the prey base of puffins experience direct mortality from increasing temperatures, decreasing salinity, or experience behavioral changes leading prey deeper than the maximum dive depth of puffins or to areas further from puffin colonies. A decrease in salinity can lead to reduced mixing in the water column, which would decrease the nutrients available to phytoplankton, the base of the marine food web in the Gulf of Maine. Fish may die, shift their range, or experience changing phenology due to changes in temperature and salinity, all of which could have major consequences for puffin colonies in the Gulf of Maine. Without a relatively predictable food base close to colonies to feed chicks, puffin colonies may experience widespread breeding failure or even colony collapse. The Gulf of Maine is currently the southern edge of the breeding distribution of puffins in eastern North America and the loss of this species and possibly other alcids in the region would represent a loss in biodiversity and a group of species which can be used as indicators of ecosystem health. Seabird colonies are often a balance among many species and the loss of one or more species at a colony can sometimes result in reduced nesting by other species.

Our study is an example of the first successful effort to describe diving characteristics of alcids in the Gulf of Maine, where puffins nesting at the edge of their breeding distribution may be more susceptible to environmental changes. We found puffins are capable of diving to at least 40 m, making an incredible number of dives each day, concentrate nearly 2/3 of their dives in the early morning and late afternoon, and forage in waters with SST of 9.6 – 12.9 °C. This information can be used by managers to identify potential foraging areas based on SST and identify prey base in the upper 40 m of the water column. A helpful addition to this study would be to collect detailed chick provisioning data paired with TDR data to better characterize dives

specific to prey type. Critical to understanding the variability in seabird diets during the breeding season would be describing characteristics of productive foraging areas in addition to SST. Our study begins to answer questions about prey acquisition in a highly dynamic marine environment. Recently, technological advances have provided the opportunity to place geographic positioning system (GPS) units on birds the size of puffins, which would allow researchers to identify discrete foraging areas and begin identifying characteristics of these locations.

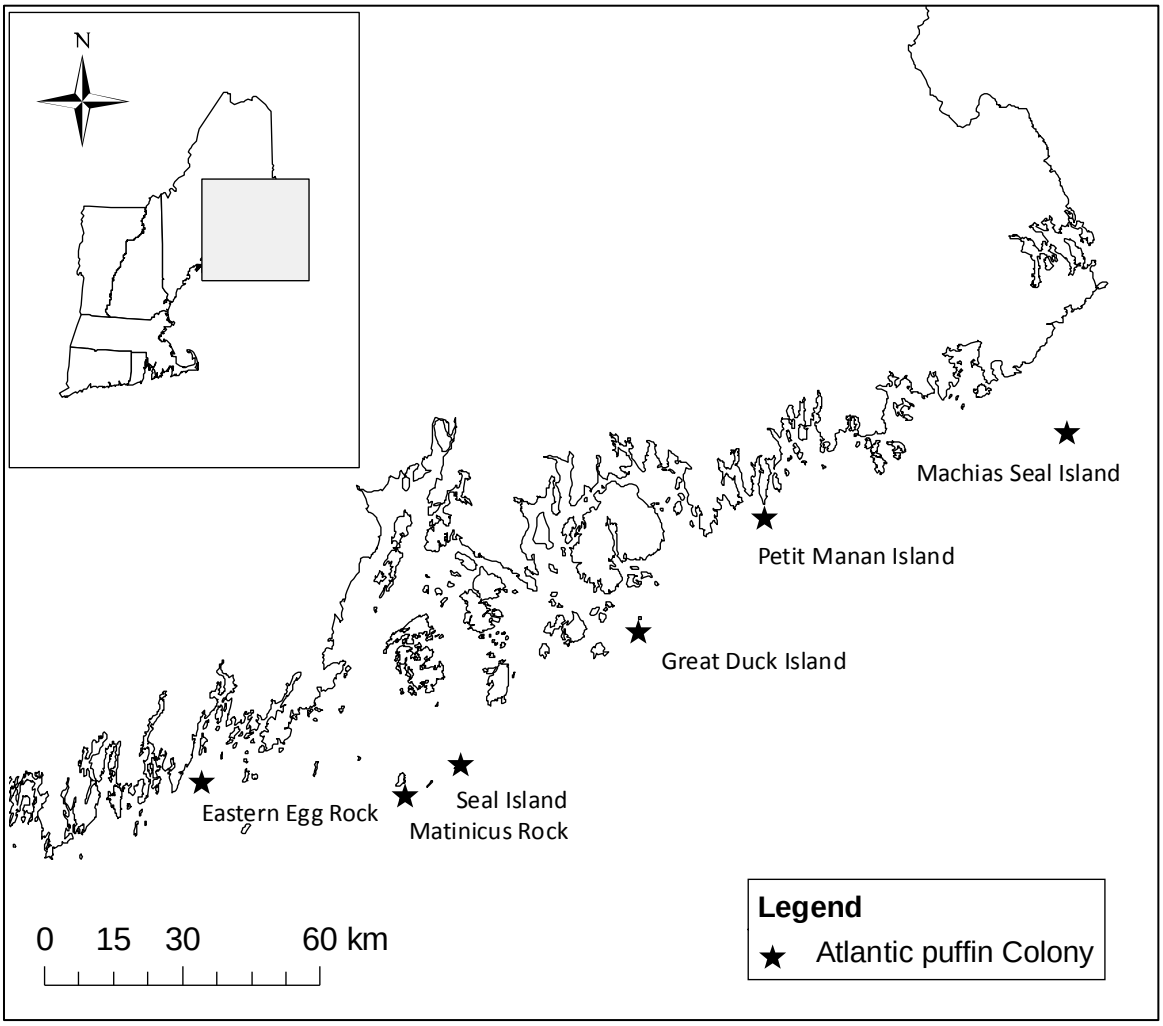

Figure 1.1. Atlantic puffin colonies in the Gulf of Maine, 2008 – 2009.

Table 1.1. Body mass changes of Atlantic puffins while they were carrying TDRs, Petit Manan Island, Maine, 2008-2009.

Bird ID	Sex	Year	Start Mass (g)	End Mass (g)	Days	Mean mass change per day (g)
CP41	F	2009	379	368	9	-1.22
CP43	F	2008	400	396	5	-0.80
CZ61	M	2008	440	455	339	0.04
CZ62	M	2008	460	469	10	0.90
CZ65	F	2008	465	412	6	-8.83
CZ69	M	2008	433	437	11	0.36
DA01	F	2009	439	445	9	0.67
DA04	F	2009	403	403	6	0.00
DA05	M	2009	445	437	6	-1.33
DA13	F	2009	385	378	10	-0.70
DA14	M	2009	430	422	10	-0.80
DA16	F	2009	437	433	9	-0.44
Mean ± SD			422.9 ± 28.4	416.0 ± 30.9		-1.01 ± 2.6

Table 1.2. Measures of Atlantic puffin productivity on Petit Manan Island, Maine, 2008-2009.

	2008			2009		
Productivity measures	TDR	Non-TDR	Pooled	TDR	Non-TDR	Pooled
No. eggs laid (e)	8	83	91	11	94	105
No. eggs hatched (h)	8	55	63	11	62	73
No. chicks fledged (f)	6	39	45	9	55	64
Hatching success (h/e)	NA	0.66	0.69	NA	0.66	0.70
Chick success (f/h)	0.75	0.71	0.71	0.82	0.89*	0.88*
Nest success (f/e)	NA	0.47	0.49	NA	0.59	0.61

*significant at $P < 0.01$ level

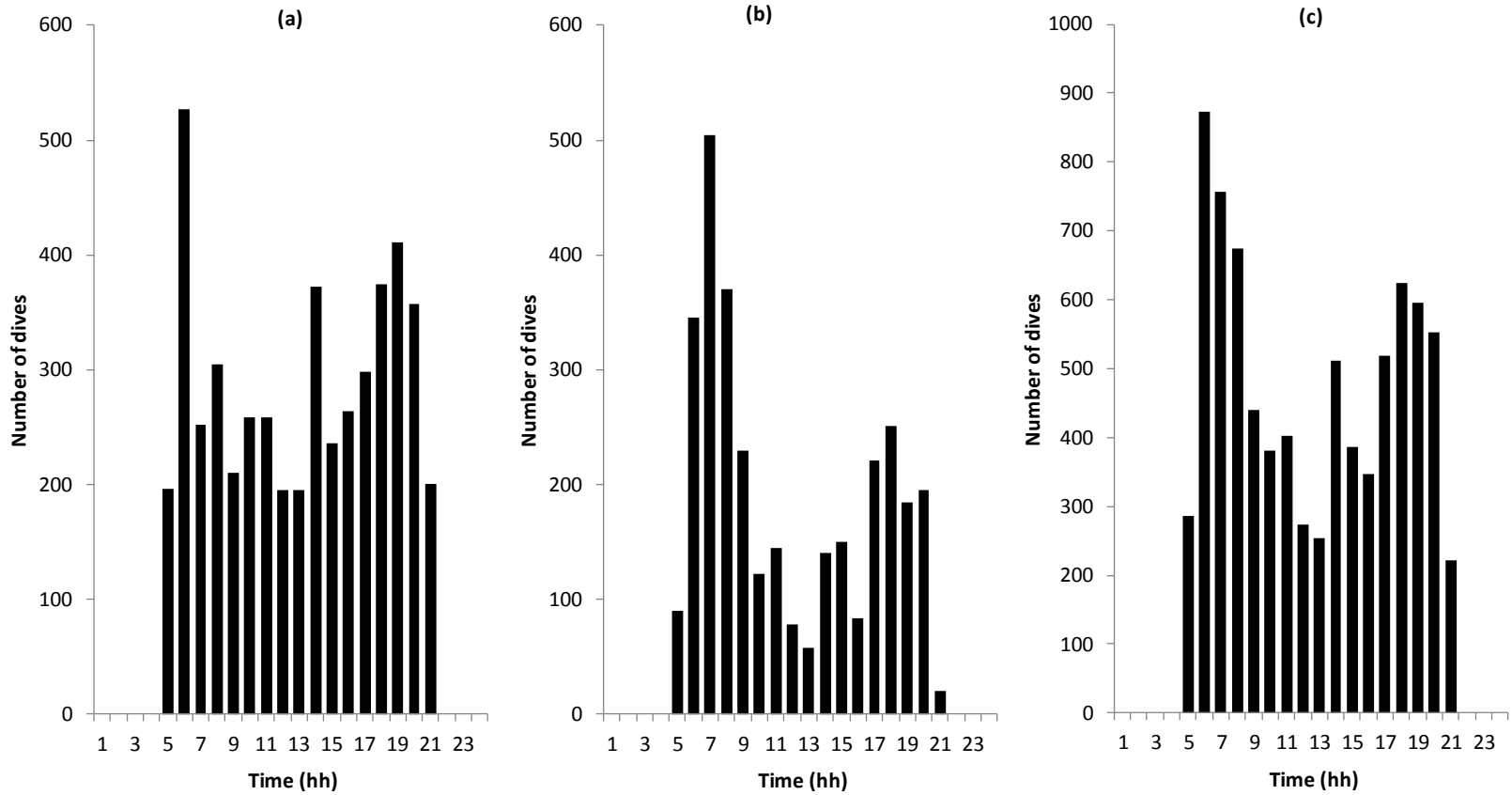

Figure 1.2. Daily timing of dives for puffins breeding on Petit Manan Island, Maine, pooled across individuals and years, 2008-2009: (a) females n = 8), (b) males (n = 5), (c) pooled (n = 13).

Table 1.3. Characteristics of dives made by Atlantic puffins on Petit Manan Island, Maine, 2008-2009.

Bird ID	Sex	Year	Days Recorded	No. of dives	Mean no. of dives per day	Percent time diving	Mean dive depth (m)	Max. dive depth (m)	Mean dive duration (s)	No. of bouts per day	Dives per bout	Bout Ending Criterion [1] (s)
CP41	F	2009	2	652	326.0	17.45	8.7	25.3	47.10	30.26	17.26	69.65
CP43	F	2008	2	561	280.5	18.91	12.2	30.0	56.40	51.76	8.28	42.32
CZ61	M	2008	2	277	138.5	5.43	10.3	23.0	48.99	21.76	10.55	58.69
CZ62	M	2008	3	493	164.3	13.34	7.6	23.0	46.11	16.86	29.16	35.3
CZ65	F	2008	2	336	168.0	10.46	7.6	18.8	49.05	34.43	17.71	48.05
CZ69	M	2008	5	1503	300.6	13.01	10.1	30.9	45.81	21.85	13.74	50.62
DA01	F	2009	3	888	296.0	20.55	8.6	22.7	42.68	31.52	16.64	58.66
DA04	F	2009	2	313	156.5	8.49	8.4	23.0	47.88	33.94	9.76	83.08
DA05	M	2009	3	380	126.7	6.95	12.7	40.7	51.31	21.08	18.26	84.27
DA06	F	2009	1	449	449.0	11.61	11.4	40.7	48.16	49.40	12.37	62.54
DA13	F	2009	3	1137	379.0	23.68	9.5	32.4	53.44	49.29	11.5	46.16
DA14	M	2009	2	534	267.0	16.66	10.7	25.8	49.63	34.19	14.47	69.48
DA16	F	2009	2	574	287.0	17.60	8.7	25.3	47.10	20.98	14.44	69.39
Mean ± SD					256.85 ± 99.6	14.16 ± 5.5	9.7 ± 1.7	27.8 ± 6.8	48.74 ± 3.5	32.10 ± 11.9	14.93 ± 5.3	59.96 ± 15.0

[1] threshold used to determine the end of one group of dives and the beginning of the next group; derived from a maximum likelihood model of a mixture of two random Poisson processes

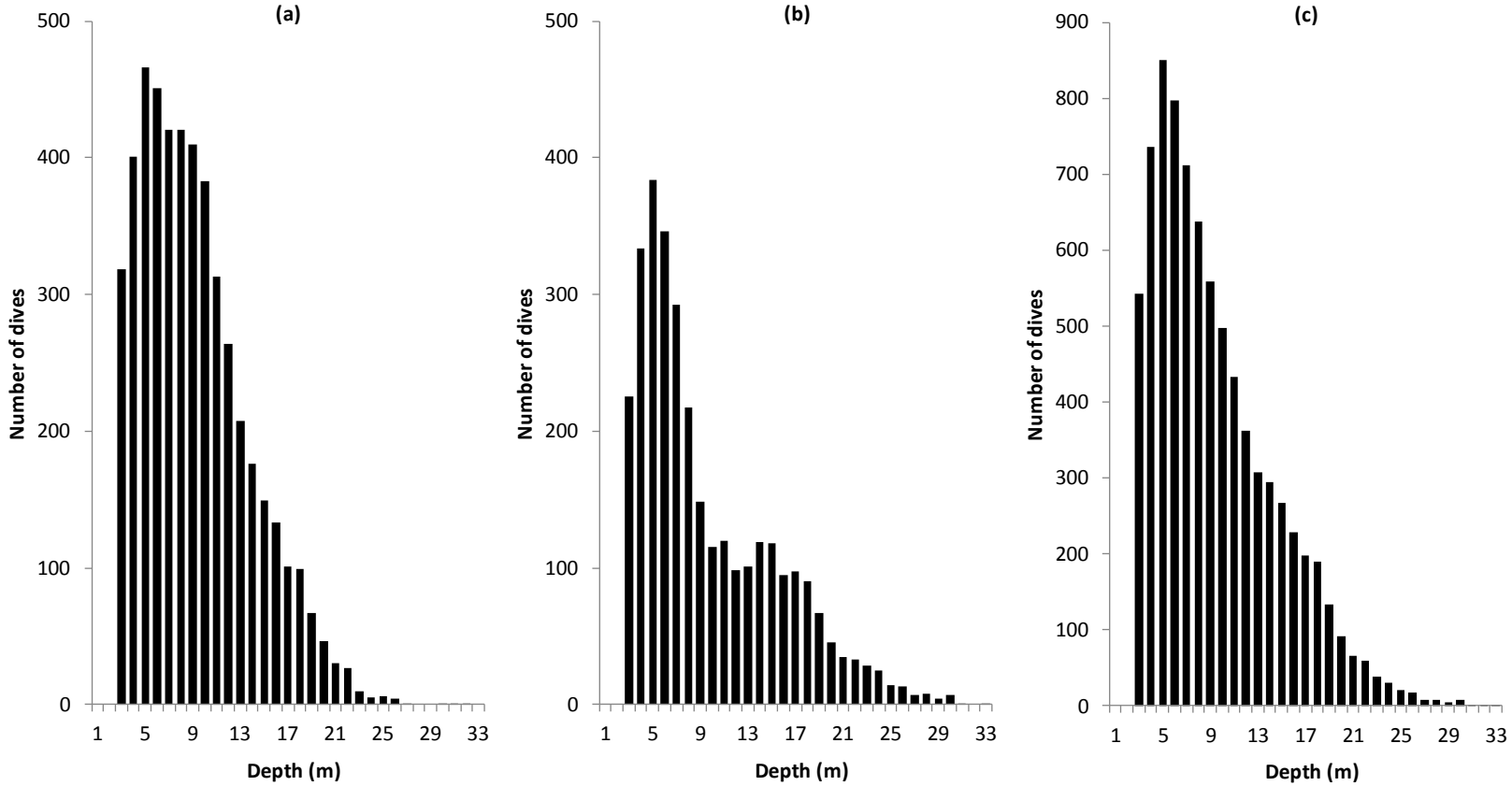

Figure 1.3. Depth frequency of dives made by male and female puffins nesting on Petit Manan Island, Maine, pooled across individuals and years, 2008-2009: (a) females (n = 8), (b) males (n = 5), (c) pooled (n = 13).

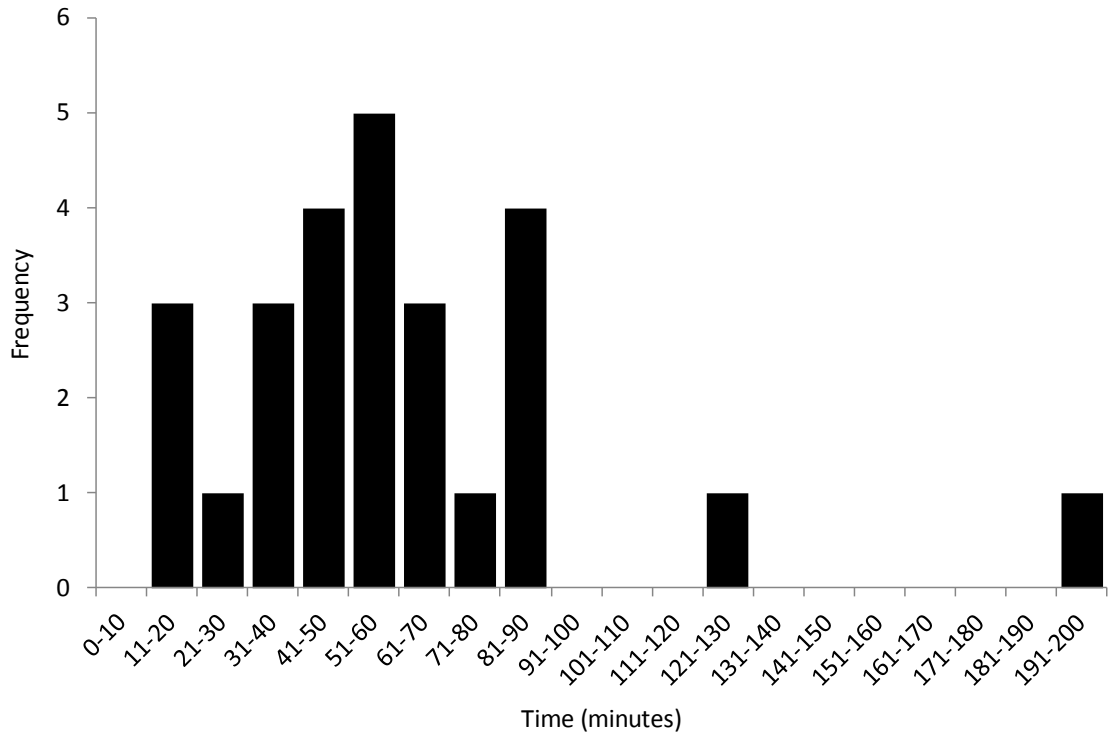

Figure 1.4. Foraging trip times for Atlantic puffins breeding on Petit Manan Island, Maine, 5-26 July 2009 (n = 26).

Figure 1.5. Estimated foraging trip distance for Atlantic puffins breeding on Petit Manan Island, 2009.

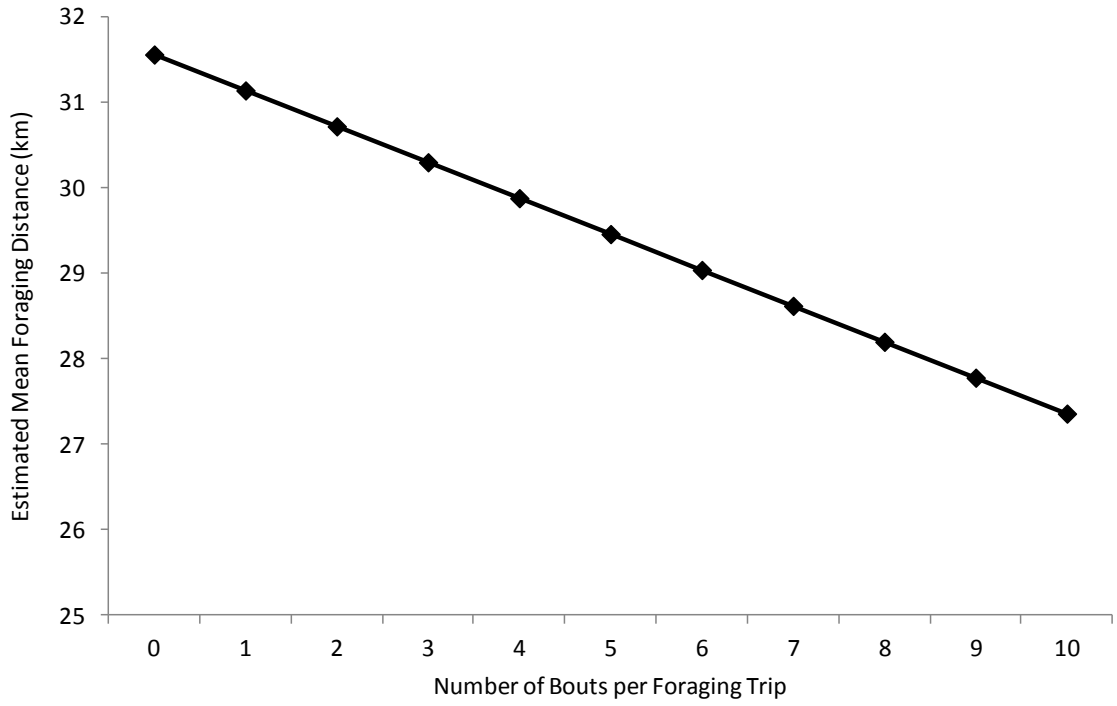

Figure 1.6. Estimated mean foraging distance based on number of bouts per trip, of puffins breeding on Petit Manan Island, Maine, 2008-2009.

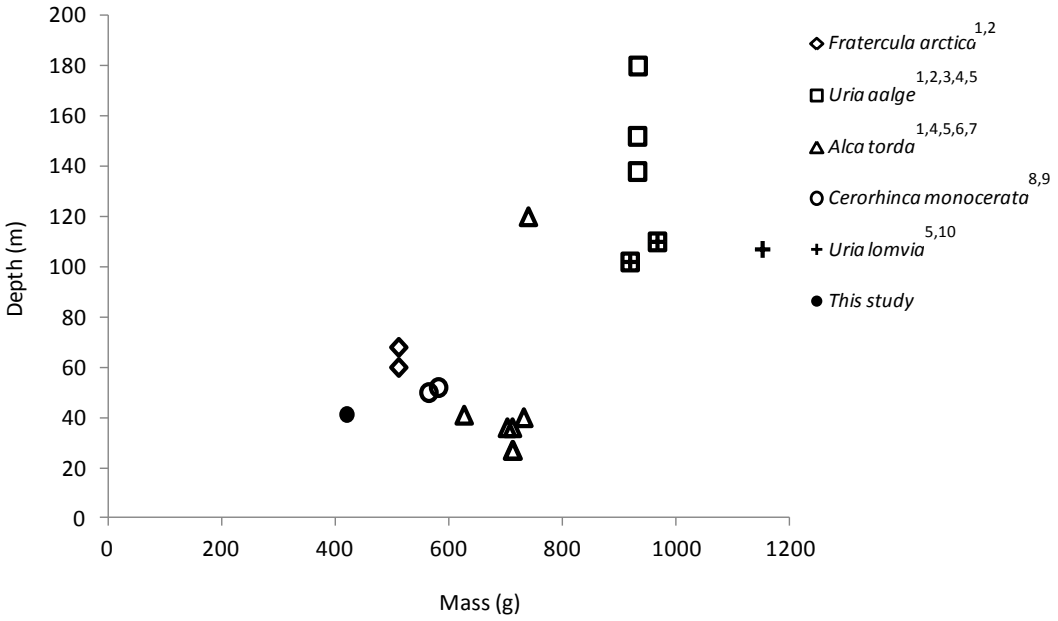

Figure 1.7. Relationship between body mass and maximum dive depth of alcids ([1]Piatt and Nettleship 1985,[2]Burger and Simpson 1986, [3]Hedd et al. 2009,[4]Paredes et al. 2005,[5]Paredes et al. 2008,[6]Dall'Antonia et al. 2001,[7]Benvenuti et al. 1998,[8]Kato et al. 2003,[9]Kuroki et al. 2003, [10]Croll et al. 1992).

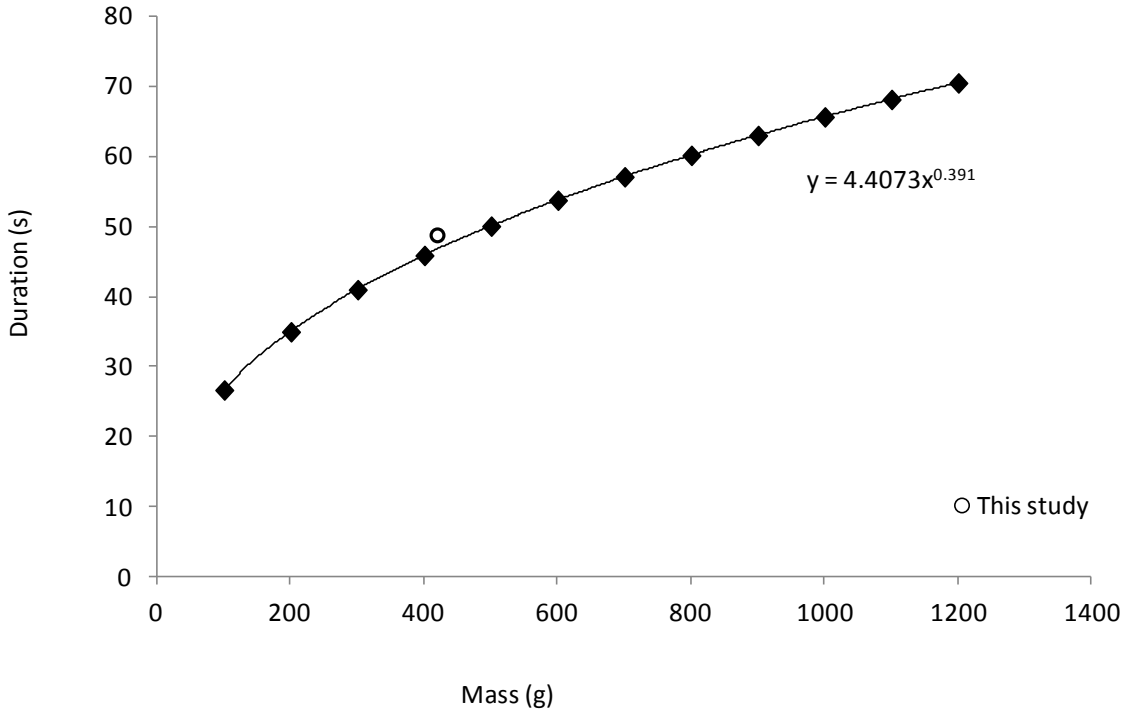

Figure 1.8. Mean dive duration of puffins nesting on Petit Manan Island, Maine 2008-2009 relative to the relationship between mass and "normal" dive duration as described by Watanuki and Burger (1999)

CHAPTER 2

NEST SITE CHARACTERSTICS OF ALCIDS BREEDING ON PETIT MANAN ISLAND, MAINE

2.1 Introduction

Atlantic puffins (*Fratercula arctica*), common murres (*Uria aalge*), and razorbills (*Alca torda*) are highly colonial alcid species which nest in a variety of habitats across their North American breeding range, from Maine, USA, to Nunavut, Canada (Gaston and Jones 1998). In the Gulf of Maine, puffins, razorbills, and common murres feed offshore and are restricted to nesting on offshore islands, where they have greater protection from mammalian predators. In contrast, black guillemots (*Cepphus grylle*) often nest on smaller islands, closer to the mainland, feed closer to shore, and usually breed in low densities. In the Gulf of Maine, puffins nest primarily in sod burrows, and cracks and crevices under rocks, black guillemots nest in openings under boulders and rocks, or marine debris washed ashore, while razorbills nest in large crevices under rocks, and common murres primarily nest under ledges formed by large rock outcrops (Gaston and Jones 1998). Although razorbills and common murres nest on open ledges elsewhere, this nesting behavior does not occur in the Gulf of Maine (Gaston and Jones 1998).

Alcids nesting in Maine have experienced drastic population changes over the last two centuries. Prior to 1870, puffins nested at five colonies (Lowther et al. 2002) and by 1870 puffins, along with closely related black guillemots, were nearly extirpated from the coast of Maine (Drury 1973). By 1902, only one breeding pair of puffins was left in Maine, breeding on Matinicus Rock (Palmer 1949), while in 1903, 75 pairs of guillemots nested on 14 islands

(Korshgen 1979). From 1973 to 1986, Project Puffin, started in 1973 by National Audubon Society, transplanted 954 puffin chicks from Great Island, Newfoundland to Eastern Egg Rock, and transplanted 950 chicks to Seal Island from 1984 to 1989. Adult puffins returned to Eastern Egg Rock in 1977 and to Seal Island in 1986, and have been experiencing a steady increase in population size in the Gulf of Maine since. Due to their breeding ecology, it is difficult to obtain accurate estimates of the number of breeding black guillemots. In 1977 there were approximately 2,700 breeding pairs in Maine (Korshgen 1979), and by 1995 they were breeding on 166 islands in the Gulf of Maine with 6,100 adults observed but an unknown number of breeding pairs. Currently, there are approximately 7,500 pairs of puffins nesting on six managed colonies in the Gulf of Maine, while approximately 1,110 pairs of razorbills nest on four managed and three unmanaged colonies in the Gulf of Maine (GOMSWG 2009a,b, GOMSWG 2011). Common murres nest only on Machias Seal Island, where a census of the colony has not been completed, while a single pair attempted to nest on Matinicus Rock in 2010 and failed. Managed colonies are sites at which biological staff are present at the colony throughout the majority of the nesting season, while unmanaged colonies have no full-time human presence during the nesting.

Alcids nesting in the Gulf of Maine are limited to areas of high prey availability during chick rearing due to the energetic needs of their offspring, combined with energetically expensive flight, resulting from their high wing loading (Balance et al. 2001). In addition, colony sites are typically limited to islands without human occupancy or mammalian predators. In the Gulf of Maine, alcids nest in a variety of materials, including deep sod burrows, open rock crevices, and in debris washed ashore. Many nests are located near the high water mark and are

therefore susceptible to flooding early in the nesting season and at other times of high wave action. In other parts of their range, the productivity of puffins and guillemots has been found to be correlated with nest-site characteristics (Divokey et al. 1974 and Nettleship 1972). Few puffin and razorbill breeding colonies exist in the Gulf of Maine, they vary widely in nesting habitat, and they may be limited in available high quality nest sites. Managers of these seabird colonies are interested in evaluating the restoration potential of islands, whether nest sites are a limited resource, and if so, how they might enhance or add suitable burrows. Here, we report on the mean diameter, orientation, substrate, and overhead cover of nests of three alcid species, test for differences in use of artificial versus natural burrows, and for black guillemots and Atlantic puffins, test for effects of nest-site characteristics on breeding success.

2.2 Methods

2.2.1 Study Area and Data Collection

During the 2009 nesting season, we observed the breeding success and burrow characteristics of Atlantic puffins, razorbills, and black guillemots at Petit Manan Island, Maine, USA (44°22'03"N 67°51'51"W). The island supports a diverse seabird colony of over 4000 pairs of common, Arctic and roseate terns (*Sterna hirundo, S. paradisaea, S. dougallii*), laughing gulls (*Larus atricilla*), Leach's storm-petrels (*Oceanodroma leucorhoa*), and common eider (*Somateria mollissima*), in addition to approximately 100 pairs of puffins, 80 pairs of black guillemots, and 4 pairs of razorbills. Historically, Petit Manan has been an important colonial seabird nesting island in the Gulf of Maine, and since 1974 has been owned and managed by the U.S. Fish and Wildlife Service (USFWS) Maine Coastal Islands National Wildlife Refuge. Terns began returning

to the island in 1984, when the USFWS initiated gull control efforts to minimize the number of gulls on the island. Puffins began nesting on the island in 1986 and the number of breeding pairs has been steadily increasing since, including a 70% increase between 2007 and 2008 (Figure 2.1). In 1984, there were 16 pairs of guillemots nesting on Petit Manan, and in 2004, razorbills began nesting on the island.

The island is 6.5 ha, is 2-4 m above sea level and consists of a cobble, boulder, and ledge berm surrounding an interior of grasses, sea angelica (*Angelica lucida*), red raspberry (*Rubus idaeus*), New York aster (*Aster novi-belgii*), tall meadow rue (*Thalictrum polygamum*), blueberry (*Vaccinium angustifolium*), beach pea (*Lathyrus japonicas*), dodder (*Cuscuta* spp.), and Canada bluejoint (*Calamagrostis canadensis*). The island has little in terms of vertical elevation or protection from wave action and many alcid burrows are flooded in storm events during the breeding season. Large storms, including hurricanes, often move large rocks and sod on the berm during the non-breeding season and sometimes during the breeding season, creating highly dynamic nesting habitat for alcids.

We searched for burrows during nest initiation and egg-laying (late May through early June) by identifying locations where puffins, guillemots, or razorbills were entering or exiting along the berm. Our efforts were aided by observations made from the 120-foot tall lighthouse on the island, and from that vantage point we recorded all potential burrow locations on aerial photographs. For puffins and razorbills, we conducted a completed census of burrows in late June, noting nest contents (egg, adult, or empty), and at the same time identified black guillemot nests, though a complete census was not conducted. To minimize nest disturbance, we used a video probing system (Peeper 2000 with Peep-A-Roo video extension, Sandpiper

Technologies, Inc.) to view the contents of burrows that could not be seen directly. All burrows were uniquely numbered and mapped using a handheld Trimble® GeoXT ™ Global Positioning System (GPS) unit.

In late July, when most chicks were old enough to thermoregulate, we inspected each burrow and recorded its contents, compass heading in degrees oriented with burrow opening, whether the burrow was naturally or artificially constructed, diameter of the entrance (measured horizontally, vertically, and diagonally in cm), and composition of overhead and substrate material in the burrow opening, tunnel, and chamber. Artificial burrows included any nests under manmade materials purposefully placed at the site, or washed ashore. The burrow chamber was differentiated from the burrow tunnel by an increase in diameter and the presence of an egg or chick. Chamber materials were identified either by touch, or by the infrared video probing system. Material composition of the substrate, and the overhead portion of the burrow, was classified as rock, wood, vegetation, sod, concrete, brick, gravel, glass, or plastic. We did not measure the distance from the burrow entrance to the center of the nest bowl, in order to minimize disturbance to the birds.

2.2.2 Data Analysis

All statistical analyses were performed in R version 2.10.1 (R Development Core Team 2009). We compared mean burrow diameter among puffins, guillemots, razorbills, and empty burrows using a Kruskal-Wallis rank sum test because of unequal group variances to determine if there was a difference in mean burrow diameter among species. We performed a Nemenyi-Damico-Wolf-Dunn post-hoc test to identify differences in burrow diameter among groups.

Empty burrows were measured to determine if they would be suitable for alcid nesting based on burrow characteristics. We tested for a difference in the use of natural versus artificial burrows by puffins and guillemots using Fisher's exact test. We used Fisher's exact test to test for a difference in cover and substrate materials of openings, burrows, and chambers of occupied versus unoccupied nests.

For each nest, we calculated hatch, chick, and nest success. Hatch success was the proportion of eggs that hatched, chick success was the proportion of chicks that fledged, and nest success was the proportion of eggs that produced chicks that fledged.

Using classification trees we developed models that predicted either hatch or nest success for each species (puffins and razorbills) based on the type of burrow, mean diameter of opening, cover and substrate of the burrow opening, tunnel, and chamber, and orientation of the burrow entrance relative to the shoreline. For guillemots with a two-egg clutch, success was defined as having at least one egg hatch, or one chick fledge. For classification trees, prior probabilities were estimated using sample size, and splitting was based on the Gini index. A v-fold cross-validation technique with four equal-sized groups for puffins and five equal-sized groups for guillemots was used to validate our model. Variables which repeatedly appeared as the first splitting variable were removed to determine if they were masking other important discriminating variables. We evaluated our models based on the percent of correctly classified samples after a v-fold cross-validation, as well as using Cohen's kappa statistic (percent classified correctly, compared to chance). We used Monte Carlo resampling to test if the correct classification rate (CCR) of our model was greater than expected under the null hypotheses of

no difference in characteristics between burrows with successful and failed hatch and between successful and failed fledging. Unless otherwise noted, all results are reported as mean ± SD.

2.3 Results

Of 58 black guillemot nests, 17 (29%) contained one egg and 41 (71%) contained two eggs, thus producing a mean clutch size of 1.71 eggs per nest. For guillemots, estimated hatch, chick, and nest success, pooled across artificial and natural burrows, was 0.49, 0.78, and 0.38, respectively (Table 2.1), while for puffins these values were 0.70, 0.88, and 0.62, and for razorbills they were 0.75, 0.67, and 0.50. Burrow type (artificial or natural) was not related to puffin hatch, chick, or nest success ($P = 0.308$, $P = 0.255$, and $P = 1$, respectively). For black guillemots, hatch and nest success were significantly greater in artificial burrows compared to natural burrows ($P = 0.01$, $P = 0.004$), but there was no difference in chick success between burrow types ($P = 1.0$).

We compared the mean opening diameter for burrows of 104 puffins, 68 guillemots, 4 razorbills, and 59 unoccupied. Mean diameter of burrow openings of puffins, guillemots, razorbills and empty burrows (17.1 ± 4.9 cm; 24.5 ± 12.7 cm; 20.7 ± 13.5 cm and 17.2 ± 6.9 cm) were significantly different ($H = 30.3782$, $df = 3$, $p < 0.0001$). Post-hoc testing revealed differences between burrow diameters of puffins and guillemots, guillemots and razorbills, and guillemots and empty burrows ($p < 0.0001$). Artificial puffin burrows had significantly smaller opening diameters than natural burrows (Artificial: 14.04 ± 3.00 cm, Natural: 17.54 ± 4.98 cm; $X^2 = -395.1266$, $df = 7$, $P < 0.0001$). Opening diameters of artificial guillemot burrows were

significantly larger than in natural burrows (Artificial: 27.53 ± 15.31 cm, Natural: 23.51 ± 11.81 cm; X^2 = -254.8187, df =7, P < 0.0001). Razorbills did not nest in artificial burrows on the island.

We characterized the materials from burrows of 104 puffins, 70 guillemots, 4 razorbills, and 56 unoccupied (Table 2.2). Overall, 85% of occupied alcid burrows and 82 % of unoccupied burrows were natural. There was no difference in the proportion of natural versus artificial burrows used by puffins or guillemots (X^2 = 3.26, df = 1, p = 0.07). For guillemots, hatch success and nest success were significantly higher in artificial burrows compared to natural burrows (P = 0.022, and P = 0.04), while chick success was similar among burrow types (P = 0.42). Puffins had similar hatch, chick, and nest success among natural and artificial burrows (P = 1.00, P = 0.16, and P = 1.0).

Rock was the only cover material in 64% of openings, 58% of tunnels, and 55% of chambers of occupied burrows. Similarly, rock was the only cover material in 64% of openings, 62.5% of tunnels, and 64% of chambers in unoccupied burrows. For occupied burrows, the next most prominent nest site cover material was wood, represented in 20%, 21%, and 23% of openings, tunnels, and chambers, respectively. Substrate material was all rock for 53% of openings, 59% of tunnels, and 42% of chambers of occupied burrows. Unoccupied burrow openings were dominated by a rock substrate, and rock or sod chamber. Tunnel substrate of unoccupied nests were made of a variety of materials, with 29% being a sod/gravel combination, 19% plastic, 14% rock, and 14% gravel. Proportion of cover materials in opening, burrow, and chamber did not differ significantly between unoccupied and occupied nests (P = 0.6286, P = 0.4774, P = 0.6980). Similarly, there was no difference in opening, burrow, and chamber substrate between unoccupied and occupied nests (P = 0.1897, P = 0.1800, P = 0.2018).

Classification tree models were not successful in predicting success of hatching or nesting in puffins or guillemots. For puffins, our final model for predicting hatch success was a five-leaved tree with a CCR of 76% (kappa = 0.34) but the data did not have sufficient discriminatory power, or we did not capture enough variation with the variables measured, to grow a tree while decreasing overall error. The final model for predicting puffin nest success was a six-leaved tree with a CCR of 73% (kappa = 0.419) and was not significantly greater than an expected CCR with no group structure ($P<0.91$). Results were similar for guillemots, where our final model for predicting hatch success was a four-leaved tree with a CCR of 84% (kappa 0.671) but was not significantly greater than an expected CCR with no group structure ($P<0.09$). For guillemot nest success, the final model had a CCR of 83% (kappa = 0.588) and was not significantly greater than an expected CCR with no group structure ($P< 0.423$).

2.4 Discussion

We observed nearly the same mean clutch size, hatching success and nest success for black guillemots as a similar study on Petit Manan Island during the 1998 breeding season (Myers 1998). In the time since the Myers study, the number of Atlantic puffins nesting on the island has increased from 17 to 105 pairs (Table 2.1). In 1995 there were 156 breeding pairs of guillemots on the island and in 2009 we estimate a minimum of 80 guillemot pairs bred on the island, although a complete census was not conducted. From 1998 to 2009, puffins have nested at sites formerly occupied by guillemots on some parts of the island, and aggressive behavior between the two species has been observed, primarily during the nest initiation period early in the breeding season. Although the number of breeding pairs of guillemots appears to have declined approximately 50% from 1995 to 2009, hatch success and chick success have remained

nearly the same. Thus, the reduction of guillemot chicks produced annually on Petit Manan Island appears to be due to a decrease in available nest sites, as a result of competition with puffins, and not a drop in nest success. This may be the result of the relative quality of individual pairs remaining the same over the 14 years between studies, as suggested for common murres (Harris et al. 1997).

Artificial nesting structures have been used with success in several alcid species, including ancient murrelets (*Synthliboramphus antiquus*) and rhinoceros auklets (*Cerorhinca monocerata*) (Gaston 1996, Wilson 1986). Alcids breeding on Petit Manan Island had significantly different burrow opening diameters suggesting artificial nesting structures need species-specific designs. The most recent artificial nesting structures designed for alcid nesting on Petit Manan Island were wooden boxes with plastic irrigation pipes of a diameter slightly smaller than the average opening diameter of puffin burrows, similar to those used by Wilson (1986). Several artificial nesting structures with openings made of this irrigation pipe have been used by nesting puffins, but not by razorbills that are likely excluded by the pipe's small diameter.

Gaston (1996) suggested that the interior of burrows is more important than the exterior in nest site selection because artificial boxes placed away from sites near trees where many ancient murrelets nested were occupied at the same rate as natural burrows near the trees. Similarly, La Cock (1988) found Magellanic penguins (*Spheniscus demersus*) burrowed preferentially in suitable substrate, suggesting substrate is an important characteristic for these penguins. Unlike these studies, we found that characteristics of burrow interiors were unrelated to hatch or nest success. It appears that in our system, nest success is controlled by other

factors such food availability, pair quality, or perhaps stochastic processes, rather than burrow characteristics.

Whether a burrow was made of natural or artificial materials did not influence hatch, chick, or nest success of puffins, but for black guillemots, hatch and nest success were greater in artificial burrows. For razorbills nesting at Skomer, Wales, pairs nesting on open ledges had lower success than those nesting under boulders or in burrows, which was attributed mainly to egg loss by predators (Hudson 1982). Also, rhinocerous auklets nesting in areas of high vegetative cover protecting them from kleptoparasitism had higher breeding success (Miyazaki 1996). Guillemots on Petit Manan Island tended to nest in burrows or crevices with much wider openings than those used by puffins, and often in locations where they were exposed to predators and visual disturbance by humans. Despite the use of sites that appear to be suboptimal, pairs had nest success rates similar to those measured 14 years earlier. The higher hatch and nest success can be attributed to increased egg survival in artificial nests, which had smaller openings than natural nests. Smaller openings could lead to decreased disturbance of incubating adults by predator and humans. Our observations suggest that guillemots leave the nest site quickly when disturbed, which could easily lead to rolled and cracked eggs.

For the burrow characteristics we measured, we found no difference between puffin and empty burrows, suggesting that we have not identified variables relevant to nest site selection by puffins, or puffins are not exhibiting selection with regard to burrows. Burrow occupancy and nest success may be more strongly influenced by adult quality, density of nests, distance to nearest neighbor, nesting synchrony, and level of human disturbance variables which have been found to have an effect on success in several alcid species, including black

guillemots (Cairns 1980), Atlantic puffins (Nettleship 1972), common murres (Birkhead 1977, Harris et al. 1997, Hatchwell 1991), and thick-billed murres (*Uria lomvia*) (Birkhead 1985). When we looked at puffin hatch success across the island, the majority of egg losses appeared to be in areas with substantial human disturbance during the breeding season. Puffin chick losses were greatest near a foghorn on the eastern shore of the island, part of which is in the most established part of the puffin colony. This site is also located beneath a lighthouse, a preferred perch of peregrine falcons (*Falco peregrinus*), the only predator known to have successfully killed adult puffins in recent years. Guillemots are much more dispersed across the colony, but a cluster of egg and chick losses near an observation blind suggest human disturbance may have played a role. Known guillemot nests along the south and western sides of the island experienced little egg failure, probably as a result of reduced human disturbance throughout the nesting season. It appears that successful puffin nests were those with the longest, most difficult to access burrows, a characteristic that may minimize human disturbance.

A detailed study of habitat characteristics and their effects on puffin breeding success on Great Island, Newfoundland gives insight into important characteristics, but may have little relevance to Petit Manan Island because of the lack of overlap in habitats (Nettleship 1972). At Great Island, breeding success was highest on sloped habitat near cliff edges, but Petit Manan has no cliffs because of its low elevation. A repeated study at Great Island, Newfoundland found breeding success was highest closer to shore and on slopes (Rodway et al. 1998), but again there is little overlap in habitat found on Great Island and Petit Manan. More work is necessary from topographically similar islands in the Gulf of Maine.

Similar to our study, Myers (2000) studied guillemots on Petit Manan Island and found no relationship between success and luminosity in the burrow chamber, distance from burrow to the high tide line, distance from the vegetation line, distance from the nearest neighboring burrow, or burrow depth. Anecdotal evidence suggests disturbance may play a role in breeding success at Petit Manan, which has been shown for puffins nesting at Great Island, Newfoundland (Rodway et al. 1996, 1998) and has been shown to impact guillemot chick growth in Quebec (Cairns 1981). In addition, although the puffin colony at Petit Manan has been established since 1986, a 67% increase in nesting pairs between 2004 and 2009 suggests the colony is relatively young and the majority of banded puffins are likely first time or inexperienced breeders. It is possible that breeding inexperience swamps out any effect of burrow characteristics, as a result of birds being more sensitive to disturbance by predators and humans, or less able to provision their young.

Management of seabird colonies where nesting habitat is limited is often a challenge when species-specific burrow characteristics are not known. Based on alcids nesting in artificial nest boxes within 1-2 years of box placement on Petit Manan Island, we believe nest sites are limited and managers may be able to increase colony size of puffins, guillemots, and potentially razorbills with the use of artificial nest boxes. On Petit Manan Island, plastic and wooden nest structures with plastic tunnels have been used by puffins and guillemots with success, while on Matinicus Rock, similar and slightly larger wooden boxes without plastic tunnels (K. Kauffman *pers. comm.*). We suggest managers focus on placement of artificial nest boxes rather than materials because we did not find any difference in the proportion of brick, gravel, metal, plastic, rock, sod, vegetation, or wood in any part of occupied versus unoccupied burrows. Nest

boxes should be created with sufficient space inside boxes for limited visibility of incubating adults from outside the box, and for protecting chicks from predators or intra- and interspecific aggression. In addition, there is some evidence that human disturbance is a factor in nest success of puffins and guillemots. Disturbance protocols should be designed to limit human activity through areas of high alcid nesting densities. Natural nest structures could be modified to offer decreased visibility into nests by humans at observation blinds where incubating alcids could be disturbed by the mere presence of a human in the blind. Lastly, artificial nest structures should be monitored by managers for as long as feasible in order to understand patterns of alcid occupation and breeding success.

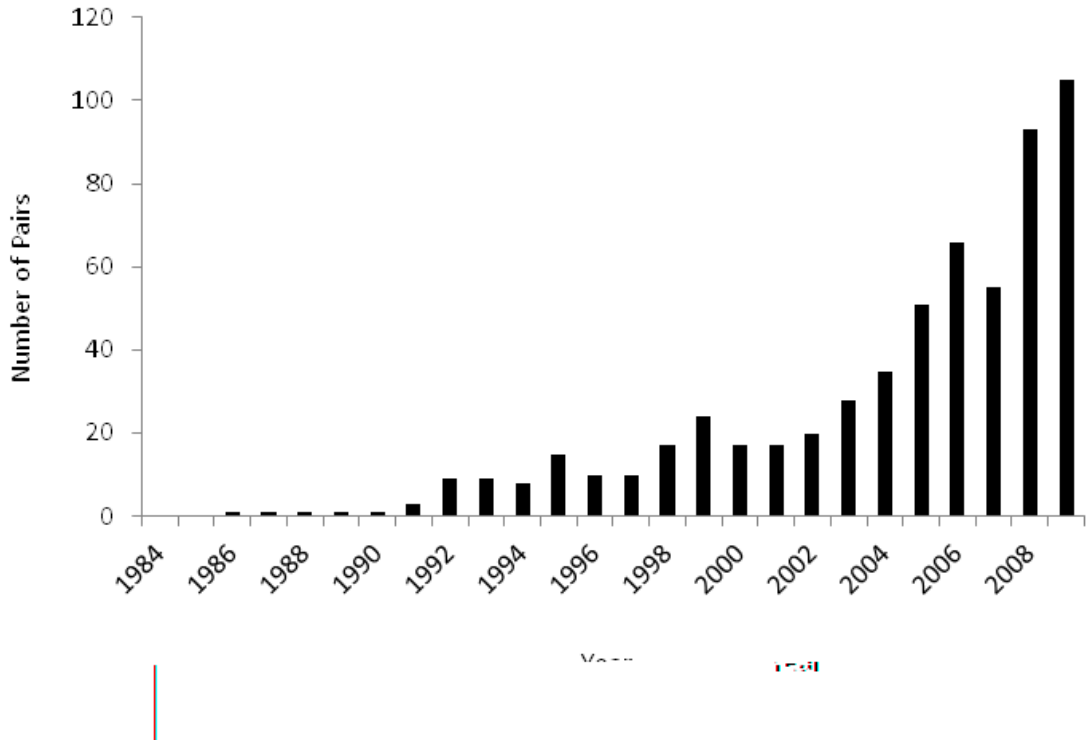

Figure 2.1. Pairs of Atlantic puffins breeding at Petit Manan Island, Maine, 1984 – 2009.

Table 2.1. Measures of alcid productivity by nest type on Petit Manan Island, Maine, 2009.

Productivity measures	Black Guillemot			Atlantic Puffin			Razorbill		
	Natural	Artificial	Pooled	Natural	Artificial	Pooled	Natural	Artificial	Pooled
No. nests (n)	46	12	58	92	12	104	4	0	4
No. eggs laid (e)	79	20	99	92	12	104	4	0	4
No. eggs hatched (h)	34	15	49	64	9	73	3	0	3
No. chicks fledged (f)	27	11	38	56	8	64	2	0	2
Mean clutch size (e/n)	1.72	1.67	1.71	1.00	1.00	1.00	1.00	0.00	1.00
Hatching success (h/e)	0.43	0.75 *	0.49	0.70	0.75	0.70	0.75	0.00	0.75
Chick success (f/h)	0.79	0.73	0.78	0.88	0.89	0.88	0.67	0.00	0.67
Nest success (f/e)	0.34	0.55 *	0.38	0.61	0.67	0.62	0.50	0.00	0.50

* significant at $P < 0.05$ level

Table 2.2. General burrow type of alcids nesting on Petit Manan Island, Maine 2009

Species	Artificial	Natural	Total
Atlantic puffin	12	92	104
Black guillemot	14	56	70
Atlantic puffin/Black guillemot	1	0	1
Razorbill	0	4	4
Unoccupied	10	46	56
Total Number of Burrows	37	198	235

CHAPTER 3

USING CLASSIFICATION TREES TO IDENTIFY SEX OF BREEDING ATLANTIC PUFFINS

3.1 Introduction

The ability to identify the sex of individuals of monomorphic species can greatly enhance our ability to interpret behavioral and ecological data. Atlantic puffins (*Fratercula arctica*), as with other members of the family Alcidae, are monomorphic and known to vary in body size throughout their breeding range (Harris 1979, Harris 1984, Moen 1991, Petersen 1976), although this variation has not been documented in North American colonies (Lowther et al. 2002). Because of this regional variation in body size, methods used to identify sex of Atlantic puffins at one colony site, may not be applicable in other parts of their geographic range.

Within alcid species, subtle differences in body size are common between the sexes (Berzins et al. 2009, Grecian et al. 2003, Jakubas and Wojczulanis 2007, Niizuma et al. 1999, Wagner 1999). Atlantic puffins are believed to exhibit such size differences (Corkhill 1972, Harris 1984), making them a possible candidate for morphometric differentiation of sexes. Discriminant function analysis (DFA) is often the statistical method of choice for differentiating sexes in seabirds, but assumptions of this parametric technique are difficult to meet, thus limiting its potential usefulness. Assumptions meet include equal group dispersions, within-group multivariate normality, no singularity or multicollinearity between variables, limited outliers, identifiable prior probabilities of group membership, and, to some extent, linear relationships among variables (McGarigal et al. 2000). Classification and Regression Trees (CART) are relatively recent nonparametric techniques that discriminate among categorical

(classification) and numeric (regression) response variables, can be used for prediction, and have fewer critical assumptions than DFA (Breiman et al. 1984, De'ath and Fabricius 2000). In our study, we used Classification Tree analysis to develop a model for predicting the sex of breeding Atlantic puffins based on morphological characteristics.

3.2 Methods

3.2.1 Study Area and Data Collection

During the 2008 and 2009 nesting seasons, we captured breeding Atlantic puffins at Petit Manan Island, Maine, USA (44° 22'03N 67° 51'51"W), a colony of approximately 100 pairs. Puffins with chicks a minimum of 7 d old were captured at nest sites using box traps, noose carpets, and by hand in 2008 (n = 20, 10 males, 10 females) and 2009 (n = 20, 9 males, 11 females). Of these 40 individuals, 18 were members of a pair in which both individuals were captured and measured. Mass was measured to the nearest 5 g using a 600 g Pesola spring scale; relaxed wing chord was measured to the nearest 1.0 mm with a 200 mm stopped ruler; and culmen (back of cere of upper mandible to tip of bill), bill depth (top of cere of upper mandible to bottom of lower mandible), bill length (of upper mandible), and head-bill (back of head to tip of bill) were measured to the nearest 0.1 mm with dial calipers. If not previously banded, each bird was banded with a metal field-readable band (Porzana, Ltd) on the right leg and a uniquely numbered U.S. Geological Survey Bird Banding Lab (BBL) metal band on the left leg. We collected one to two drops of blood (0.05 - 0.10 ml) from the tarsometatarsal or brachial vein using a 26 gauge needle and capillary tube, and transferred the blood directly onto a dot-blot card. Each card was air dried and placed in a sealed plastic bag. Samples were shipped to

Avian Biotech International, Tallahassee, FL, for sex identification using DNA polymerase chain reaction (PCR) analysis on the CHD1 gene (Devlin et al. 2004, Fridolfsson and Ellegren 1999, Grecian et al. 2003).

3.2.2 Data Analysis

To determine the number of breeding pairs in which the male was larger than the female, we compared measurements from individuals within known pairs. Comparisons were made with regard to wing chord, culmen, bill depth, bill length, and head-to-bill length. Mass was excluded from all comparisons because it was too variable within each sex. We assumed PCR analysis correctly identified the sex of individuals and then developed classification tree models using all morphological variables, except body mass, as predictor variables.

Model building, cross validation, and Monte Carlo resampling techniques were performed using R version 2.10.1 (R Development Core Team 2009). Prior probabilities were estimated using sample size (0.475 for males, 0.525 for females) and the Gini index was used for splitting. A v-fold cross-validation technique, with four equal-sized groups, was employed to validate our model. Variables which repeatedly appeared as the first splitting variable were removed to determine if they were masking other important discriminating variables. We evaluated our models based on the percent of correctly classified samples after a v-fold cross-validation, as well as using Cohen's kappa statistic (percent classified correctly, compared to chance). We used Monte Carlo resampling to test if the correct classification rate (CCR) of our model was greater than expected under the null hypothesis of no morphometric differences between males and females (Grace and McCune 2002).

3.3 Results

Differences between sexes in culmen and head-bill length were highly significant ($p < 0.001$), bill length and bill depth were significant ($p = 0.0115$ and $p = 0.002$), and wing chords were similar ($p = 0.2842$) (Table 3.1). Within pairs, males always had a larger culmen, bill length and head-bill length, while overall, males had a significantly larger mean culmen, bill depth, and head-bill length ($n = 6$, all $p < 0.01$, Table 3.2).

Our final model for predicting sex of puffins was a two-leaved tree with a CCR of 85% (kappa = 0.695) which was significantly greater than the CCR for a model with no group structure ($P < 0.009$). Our model correctly classified all females, and incorrectly classified six males (31.6 %) as females. Culmen was used as the primary splitting variable (Figure 3.1), and the CCR did not improve when culmen was removed from the model. The classification tree predicted 85% of birds with a culmen < 48.4 mm to be females, 100% with a culmen ≥ 48.4 mm and bill depth ≥ 39.15 to be males, and 57% with a culmen ≥ 48.4 mm and bill depth < 39.15 to be females.

3.4 Discussion

We found significant differences in mean morphological traits between male and female Atlantic puffins, as well as differences between members of a pair. We were able to correctly identify the sex of 85% of our sampled puffins based on culmen length and bill depth, without using information on pair membership. With one exception, all misclassified males were more than one SD smaller than the mean for at least two morphological measures of males. Thus, our model performs well, except for relatively small males and large females. Within Atlantic puffin

pairs, there was clear evidence for assortative mating, as found by others (Corkhill 1972, Wagner 1999), with females preferring males with relatively larger culmens, bill lengths, and head-bill lengths.

Correct identification of sex in alcids using DFA is typically high, though misclassification errors do occur as a result of morphological overlap between relatively small males and large females. Using DFA, correct classification rates for alcids have been reported as 91% for black guillemots (*Cepphus grylle*) (Berzins et al. 2009), 70 % of dovekie (*Alle alle*), and 80 % of razorbills (*Alca torda*) (Grecian et al. 2003, Jakubas and Wojczulanis 2007, Wagner 1999). Our CCR for Atlantic puffins, based on CART analyses, was 85%, and thus similar to rates estimated using DFA for other alcids. Because CART has fewer assumptions, it may be the more appropriate analysis in many cases where responses do not meet the assumptions of DFA.

To our knowledge, this is the first application of classification tree analysis for predicting sex of seabirds. Past studies have exclusively used DFA to develop predictive models of sex of monomorphic seabirds, but this approach may not always produce reliable results because its assumptions are difficult to meet. The most robust DFA results are obtained with large sample sizes, often difficult to obtain with a single observer. If additional observers are recruited to obtain a larger sample size, this benefit may often be out-weighed by increased measurement variation among observers. In addition, DFA requires equal group dispersions, multivariate normality within groups, no singularity or multicollinearity between variables, independent random samples and limited outliers, identifiable prior probabilities of group membership, and, to some extent, linear relationships among variables (McGarigal et al. 2000). DFA also requires complete data with no missing values for either dependent or response variables. In contrast,

CART requires only independent random samples and identifiable prior probabilities. Another important distinguishing characteristic between the two methods is the ability of CART to incorporate missing data. This is important because field studies are often plagued by mistakes in recording and transcribing data yet CART allows for samples with missing values to be used. Lastly, the output tree of CART is easy to interpret, making it advantageous to apply in the field.

In Atlantic puffins, differences in incubation time, chick feeding, and burrow maintenance and defense are related to gender (Creelman and Storey 1991), therefore we need a reliable method of identifying sex of puffins without the constraint of collecting blood or feather samples from individuals. In addition, sex differences in foraging and breeding behavior have been documented in other alcids, including common murres (common guillemot, *Uria aalge*) and razorbills, which show differences in prey species delivered, shape, depth and duration of dives, time of foraging, time spent at the colony, and length of diving bouts (Paredes et al. 2008). Sex differences have also been documented in thick-billed murres (Brünnich's guillemot, *Uria lomvia*), including number of deliveries to the chick, time of foraging, time spent with the chick at night, trip duration, number of dives per trip, and distance traveled on foraging trips (Thaxter et al. 2009).

Current models for predicting Atlantic puffin gender have been developed for several colonies across the North Atlantic using either DFA or CART (this study). A DFA to identify sex of puffins at Skomer Island (Wales), used bill depth and length and correctly classified 90% of males and 88% of females (Corkhill 1972). Similar DFAs were developed from drowned puffins at Gull Island (Newfoundland), and breeding birds at Isle of May and St. Kilda (Scotland) and Skomer Island (Wales), but the functions and correct classification rates were not reported

(Creelman and Storey 1991, Harris 1984). Our CART analysis was based on birds measured at one of five managed puffin colonies in the Gulf of Maine and correctly classified the gender of 85% of our sample. During our study, other researchers measured 86 birds at three of the remaining four colonies in the Gulf of Maine, but due to the high variation in measurements among islands, we restricted our model building to data collected by a single observer at Petit Manan Island. Future attempts at discriminating gender of Atlantic puffins should investigate whether island to island variation in morphological measurements represents true colony-specific differences in body size, or are the result of variation between observers. We agree that variation in body size between Atlantic puffins from geographically distant colonies probably represents true variation across their range (Harris 1979, Harris 1984, Moen 1991, Petersen 1976), but we suspect that island to island variation on small spatial scales, such as the Gulf of Maine, may be due to measurement variation between observers.

Table 3.1. Morphological measurements (mean ± SD) of Atlantic puffins (n = 40) nesting on Petit Manan Island, Maine, 2008-2009.

Morphological trait	Sex		Statistic	
	Male (mm)	Female (mm)	t-value	p-value
Wing chord	162.2 ± 5.7	160.3 ± 5.1	1.09	0.284
Culmen	49.3 ± 1.3	47.2 ± 1.9	4.07	<0.001
Bill length	31.6 ± 1.7	30.3 ± 1.2	2.68	0.012
Bill depth	40.0 ± 1.3	37.9 ± 2.6	3.31	0.002
Head-bill	82.2 ± 1.6	79.5 ± 1.4	5.26	<0.001

Table 3.2. Sex-specific variation of morphological traits within pairs of Atlantic puffins (n = 9 pairs) nesting on Petit Manan Island, Maine, 2008-2009.

Morphological trait	Males larger (percentage)	P-value (paired t-test)
Wing chord	67	0.0001
Culmen	100	0.0031
Bill length	100	0.0110
Bill depth	78	0.0004
Head-bill	100	0.0011

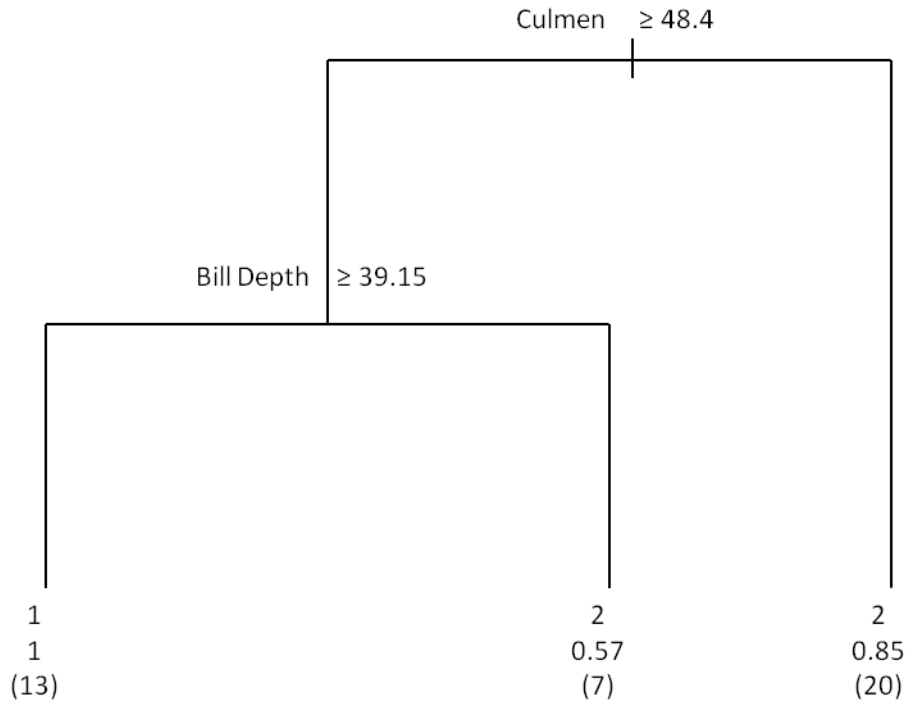

Figure 3.1. Classification tree for Atlantic puffins breeding on Petit Manan Island, Maine. Note: If the statement is true, move left. Nodes report group (1 = Male, 2 = Female), purity of node (proportion of correctly identified samples), and number of samples in the node.

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